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WHAT IS THE LEAF BEETLE *CALLIGRAPHA SCALARIS* (LECONTE)?

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ABSTRACT. Since the description of *Calligrapha scalaris* (LeConte, 1824), a leaf beetle reported as an occasional serious pest of American elm, this taxon has been affected by remarkable taxonomic confusion. Most authors have invoked their particular and generally flawed concept of *C. scalaris* (LeConte) without reference to John E. LeConte's type material at the Museum of Comparative Zoology (Cambridge, Massachusetts). In this study, I have revised the series for *C. scalaris* (LeConte) conserved as part of J. LeConte and G. Horn collections, and confirmed that it includes as many as nine *Calligrapha* species, most of them lacking an association with *Ulmus*. Among these specimens, a couple of them from Texas are recognized as generally consistent with the original description and the only potentially elm-feeding animals. Thus, despite legitimate doubts for their availability to J. LeConte at the moment of the species description, they are designated here as neo- and paraneotypes, respectively, in an effort to maximize taxonomic stability. The species is redescribed on the basis of the neotype and diagnosed from all other species in this group, defined here as the "Calligrapha scalaris" group, including a provisional identification key for 14 species and for specimens conforming to the respective types. Finally, the study of syntype material from the Museum für naturkunde (Berlin) of *C. multiguttis* (Stål, 1865), an early synonym of *C. scalaris* (LeConte), allowed recognition of several other *Calligrapha* taxa affected by this synonymy, including *C. ignota* Brown, *C. knabi* Brown, and *C. tiliae* Brown (= *Chrysomela multiguttis* Stål [pars] **nov. syn.**).

INTRODUCTION

Since I started to study the biology, evolution, and, more recently, systematics of the leaf beetle genus *Calligrapha* Chevrolat, 1836 (Gómez-Zurita, 2005; Gómez-Zurita *et al.*, 2004, 2006; Montelongo and Gómez-Zurita, 2013, 2014), no other species has been more problematic for its identification in collections than *C. scalaris* (LeConte, 1824). Every author in every collection seems to interpret this taxon in a slightly different way, "a matter of individual opinion", as pointed out by Knab (1909). The difficulties associated with this taxon were nicely illustrated by W. J. Brown (1945), who demonstrated the existence of a species complex of very similar entities, at least morphologically,

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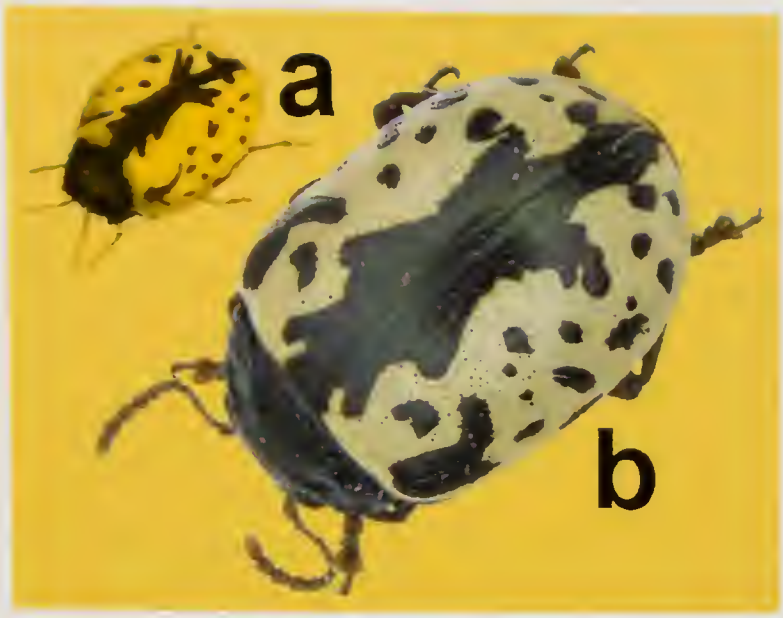

Figure 1. a, John Eatton LeConte's artistic rendition of the species *Chrysomela scalaris* in the original 1824 publication, and b, a mounted specimen of *Calligrapha scalaris* (LeConte) collected on *Ulmus* in Oklahoma, SW of Crawford, Spring Creek Lake, 24 June 2011, T. Montelongo leg. (IBE-JGZ voucher no. C326).

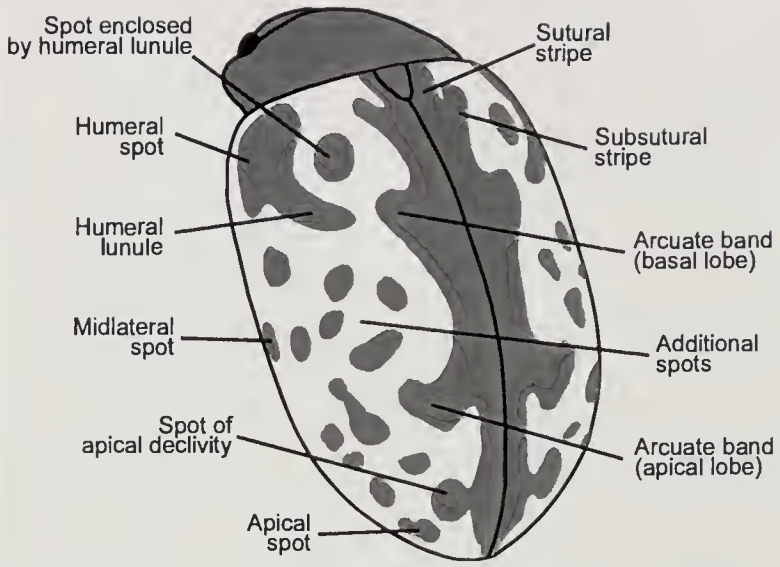

Figure 2. Elytral spot nomenclature in a typical species of the *Calligrapha scalaris* (LeConte) group (redrawn from figure 67 in Wilcox, 1972).

that nevertheless differed strikingly in their ecologies, and even in their reproductive biologies, for some species are thelytokous. This author described several new species around *C. scalaris* and tried to provide morphological arguments for their separation, yet the chief character to distinguish them remained almost exclusively the knowledge about their host plant (Brown, 1945; Wilcox, 1972). Unfortunately, this information is not available for most collection specimens, which therefore remain unidentifiable, at least until diagnostic characters still preserved in dry collection specimens are discovered.

John Eatton LeConte (1824) described *Chrysomela scalaris* on the basis of color and also highlighted two conspicuous elytral markings, namely a moon-shaped humeral marking and a broad sutural dentate marking; he also provided an illustration (drawn by himself; Fig. 1) and mentioned the occurrence of the species from New York to Florida. These characters were more than sufficient to distinguish the new species from all other Nearctic *Chrysomela* Linnaeus, 1758 known at that time, particularly the ones that would be treated as *Calligrapha* in the future. However, as the Nearctic fauna was being scrutinized, new species were described belonging to this group of animals and soon the "diagnostic" characters for *Calligrapha scalaris* proved insufficient, resulting in the remarkable taxonomic confusion occurring today for this species. Indeed, LeConte's characters correspond respectively, in the nomenclature of Wilcox (1972), to confluent humeral spot and lunule, and to sutural and subsutural stripes fused together with the arcuate band (Fig. 2). These characters are shared by at least 13 currently accepted North American taxa (and many southern Nearctic and Neotropical species, as well). Thus, every collection ranks under *C. scalaris* a large variety of forms, sometimes not even presenting these features.

In the volume on insects of the series *Fauna Boreali-Americana*, published well over a decade after the description of *C. scalaris*, its author, Reverend W. Kirby, ignored this species and initiated the confusion surrounding the taxon (Kirby, 1837). The description offered by this author for *Calligrapha philadelphica* (Linnaeus, 1758)[2]

[2] This taxon represents another taxonomic conundrum which shall be dealt with in a separate study.

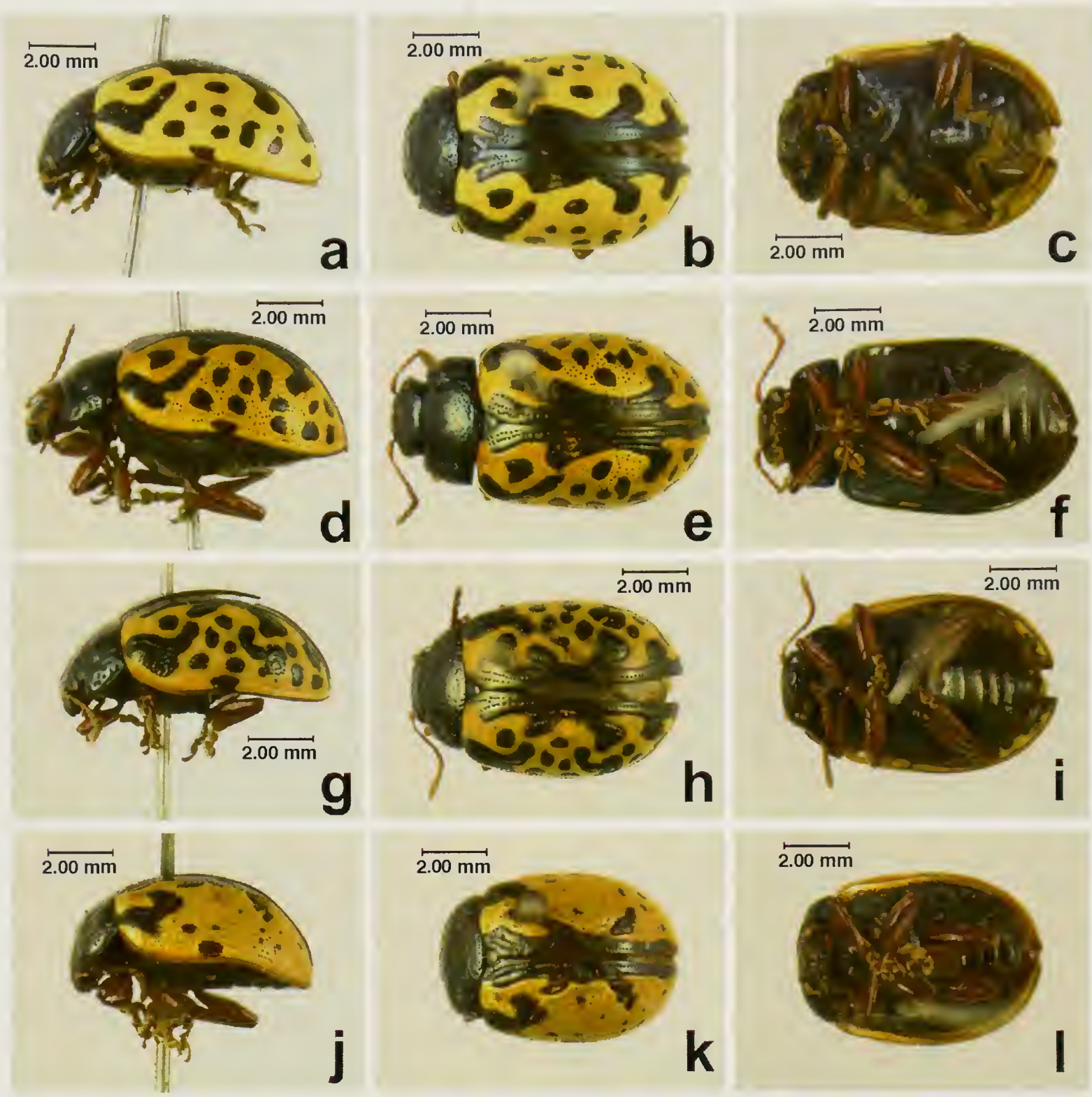

Figure 3. Lateral, dorsal, and ventral views of "*Chrysomela scalaris* LeConte" examples in LeConte and Horn Collections (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts): a–c, *Calligrapha ostryae* Brown; d–f, *C. ignota* Brown; g–i, *C. floridana* Schaeffer; and j–l, *C. rowena* Knab. Scale bar = 2.0 mm.

fits better the one for *C. scalaris* or allied species in highlighting the "longitudinal stripe at the suture with three obsolete branches", a feature clearly missing in *C. philadelphica*. Indeed, he mentioned another feature for this species exclusive for one of the members of the *scalaris*-group: "epipleura dark-green", only found in *C. ignota* Brown, 1945 (Fig. 3f). In addition, two varieties were mentioned that are currently recognizable as different species with pale epipleura: one being perhaps the true *C. philadelphica* (var. B), and one seemingly with the apex of the arcuate band detached from the subsutural stripe (perhaps *Calligrapha rowena* Knab, 1909; var. C). Even though Kirby's (1837)

concept of *C. philadelphica* did not possibly include the true *C. scalaris*, Rogers (1857) identified part of the confusion and synonymized the former with LeConte's taxon, a decision that was retained in all subsequent catalogues. Rogers (1857) knew *Chrysomela scalaris* LeConte from the Middle States, Nebraska, and Lake Superior, and figured a specimen very much fitting the concept for this species used by subsequent authors (but see below). Suffrian (1858), in his annotated translation of the previous work, reported this species from many other localities in North America such as Louisiana and Texas, but also as far south as Mexico and Costa Rica, obviously misidentifying some of the Neotropical species with *Calligrapha scalaris*. His description of the sutural marking raises again suspicion of his merging under LeConte's species of several forms later recognized as different species. This author also cited Harris' (1841) work on New England pest insects to highlight the association of this species with elm and linden. In his 13th division of *Chrysomela*, in section C (typical North American *Calligrapha*), Stål (1865) proposed a new name, *Chrysomela multiguttis*, for LeConte's *C. scalaris*, to avoid homonymy with *Doryphora scalaris* Olivier, 1807, placed also in the genus *Chrysomela* Linnaeus under Stål's lax taxonomic concept for American Chrysomelinae (Horn, 1884). Immediately after, the name fell as synonym and appeared in catalogues under *Calligrapha scalaris* again (e.g., Gemminger and Harold, 1874; Horn, 1884). Jacoby (1880–1892) reported the species from Mexico and offered a comparison with a strikingly different southern Nearctic and Neotropical species, *Calligrapha diversa* Stål, 1859. The drawing appearing in *Biologia Centrali-Americana* (table 11, fig. 6 *in* Jacoby, 1888–1892, Suppl.) was based on a specimen apparently collected in Mexico by M. Boucard; the appearance of this beetle is similar to the *C. scalaris*-like animals found in northeastern North America and studied by Brown (1945), very different from the elm-feeding *Calligrapha* in southern North America, and thus the Mexican record could be a labeling mistake. Taking a lumper stand to an extreme, and misguided by the confusing taxonomic situation affecting *Calligrapha*, also regarding their ecology (e.g., Hagen, 1884), Angell (1885) proposed that *C. scalaris* was but a variety or race of *C. philadelphica* by name priority rules. However, judging from the drawings in this article, G. Angell ranked under this name all North American *Calligrapha* known at that time plus several others that would be recognized later. His proposition was criticized, although interestingly not based on the diagnosis of the existing objective morphological differences, but on the experience in collecting different-looking animals on different plants (Caulfield, 1885). The prevailing taxonomic disorder and the lack of knowledge about the importance of ecology separating these species jeopardized biological interpretations affecting them, such as Whitehead's (1918) very detailed description of the life cycle of a *Chrysomela scalaris* LeConte appearing in large numbers on *Alnus* trees in Nova Scotia. This author indeed endorsed the idea of this species feeding upon several trees, not only elms and lindens as early proposed by Suffrian (1858). Knab (1909) also associated LeConte's *Calligrapha scalaris* with elm and linden, and he was the first to split the *C. scalaris* (LeConte) concept to recognize two new taxa: *Calligrapha rhoda* Knab, 1909 (Figs. 4d–f) and *Calligrapha rowena* (Figs. 3j–l). This author put the emphasis on these species' food plants, hazel and dogwood, respectively, as well as several morphological differences. Years later, Schaeffer (1928) described *Calligrapha confluens* (Figs. 4a–c), a species

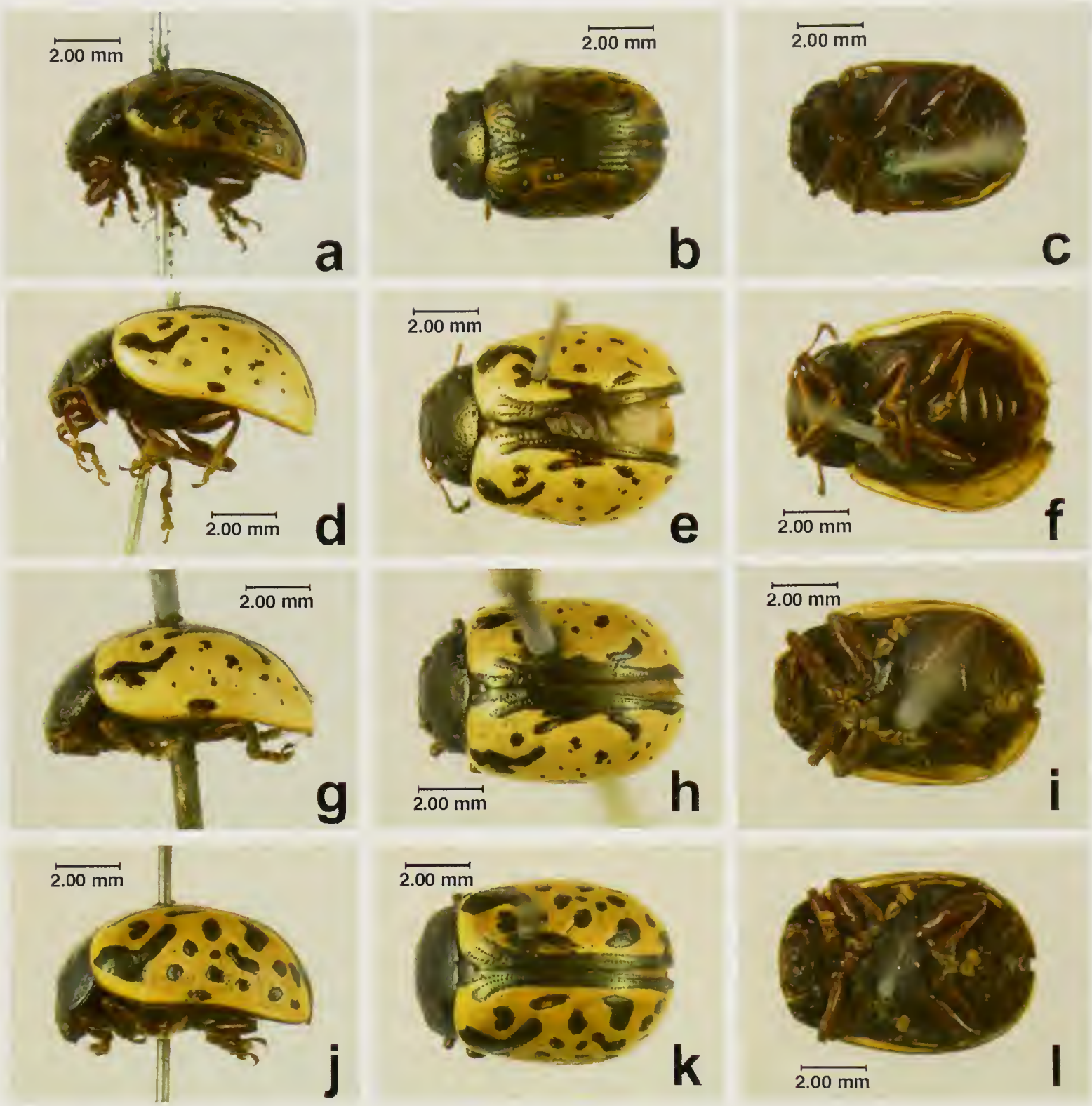

Figure 4. Lateral, dorsal, and ventral views of "*Chrysomela scalaris*" LeConte examples in LeConte and Horn Collection (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts): a–c, *Calligrapha confluens* Schaeffer; d–f, *C. rhoda* Knab; g–i, *C. pruni* Brown; and j–l, *C. dolosa* Brown. Scale bar = 2.0 mm.

associated with alder, and clearly divergent from *C. scalaris*. This species was the same studied by Whitehead (1918), as easily deduced from host plant data but also thanks to the superb drawings presented in the latter work. The description of *C. confluens* Schaeffer, 1928 diagnosed it from *C. scalaris* in recognizing that the arcuate band is not bent forming an apical lobe and that most specimens have the suture pale at the apical declivity of the elytra. The list of type specimens mentions one individual collected on alder, the plant where this species lives (Brown, 1945), but the author did not elabo-

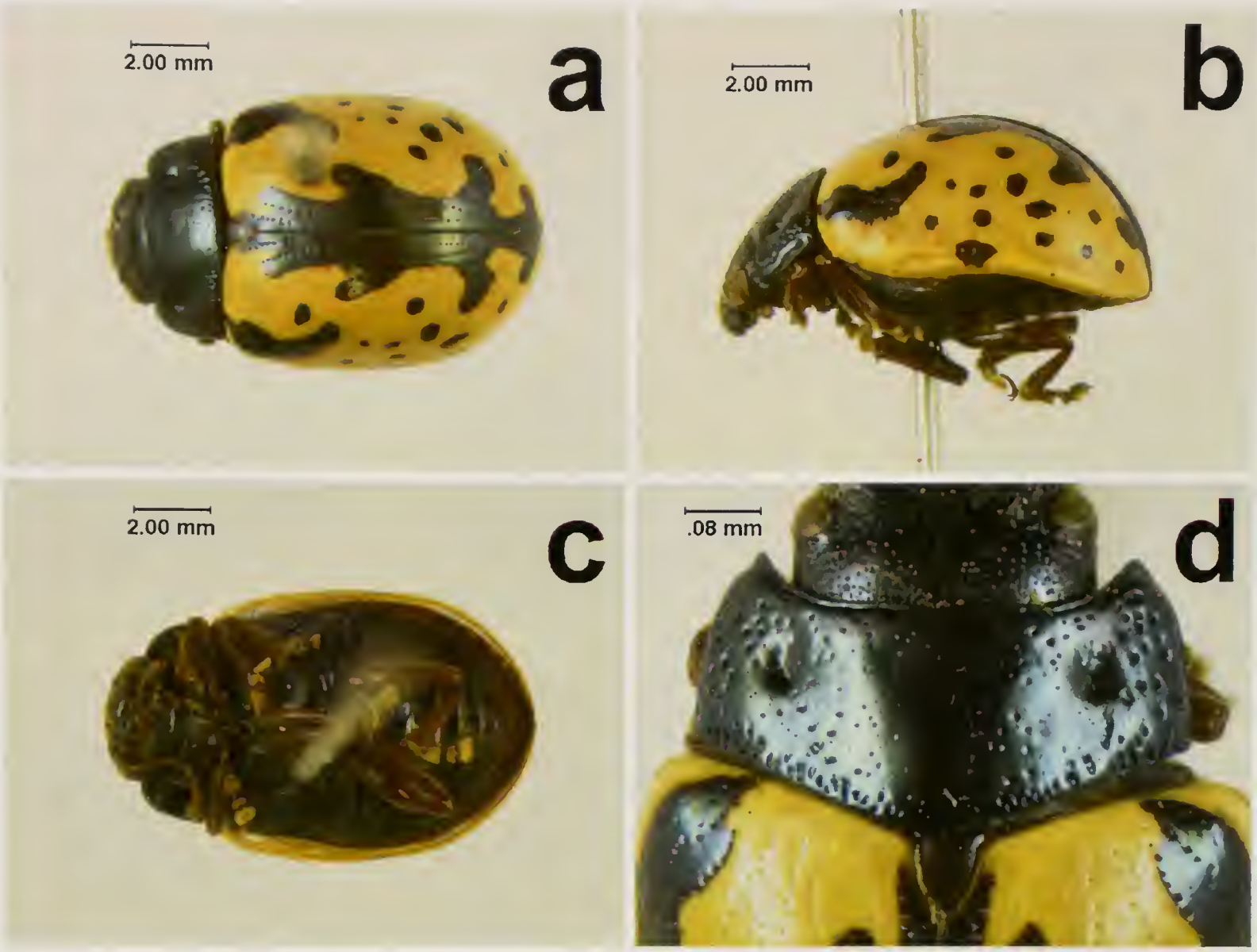

Figure 5. Neotype of *Calligrapha scalaris* (LeConte) in a, dorsal; b, lateral; and c, ventral views (scale bars = 2.00 mm), with d, detail of the pronotum (scale bar = 0.80 mm).

rate on this important ecological difference. The same author described *C. scalaris* var. *floridana* Schaeffer, 1933 (Figs. 3g–i), putting the emphasis in the comparison with *C. rhoda*, perhaps misguided by F. Knap's label attached to the type specimen, "rhoda var. floridana", since this species is very similar, indistinguishable some may think, from the typical *C. scalaris*. However, the chance that this is a sibling species of *C. scalaris* is possible, as it seemingly feeds on *Cornus* (Peck and Thomas, 1998; also, pers. obs.), but has also been reported from wax-myrtle (genus *Myrica*; Blatchley, 1924). The next author to recognize a different species within the group of *Calligrapha* with broad "dentate" sutural markings was Brown (1940), who described *C. knabi*, another *Cornus*-feeding species, very similar in fact to Knab's *C. rowena*, from which it can be recognized by a suite of relatively constant characters in both species, including the basal spot of the arcuate band not completely fused laterally to the subsutural stripe in *C. knabi* Brown, 1940, as well as slightly divergent basal ends of paired spots enclosed by the humeral lunule in this species (generally as U-shaped marking as opposed to the more roundish spot in *C. rowena*), or the more numerous and larger additional spots on the disc of elytra in Brown's taxon (compare Fig. 6a with Fig. 3k). Finally, Brown (1945) made a thorough revision of this group, paying

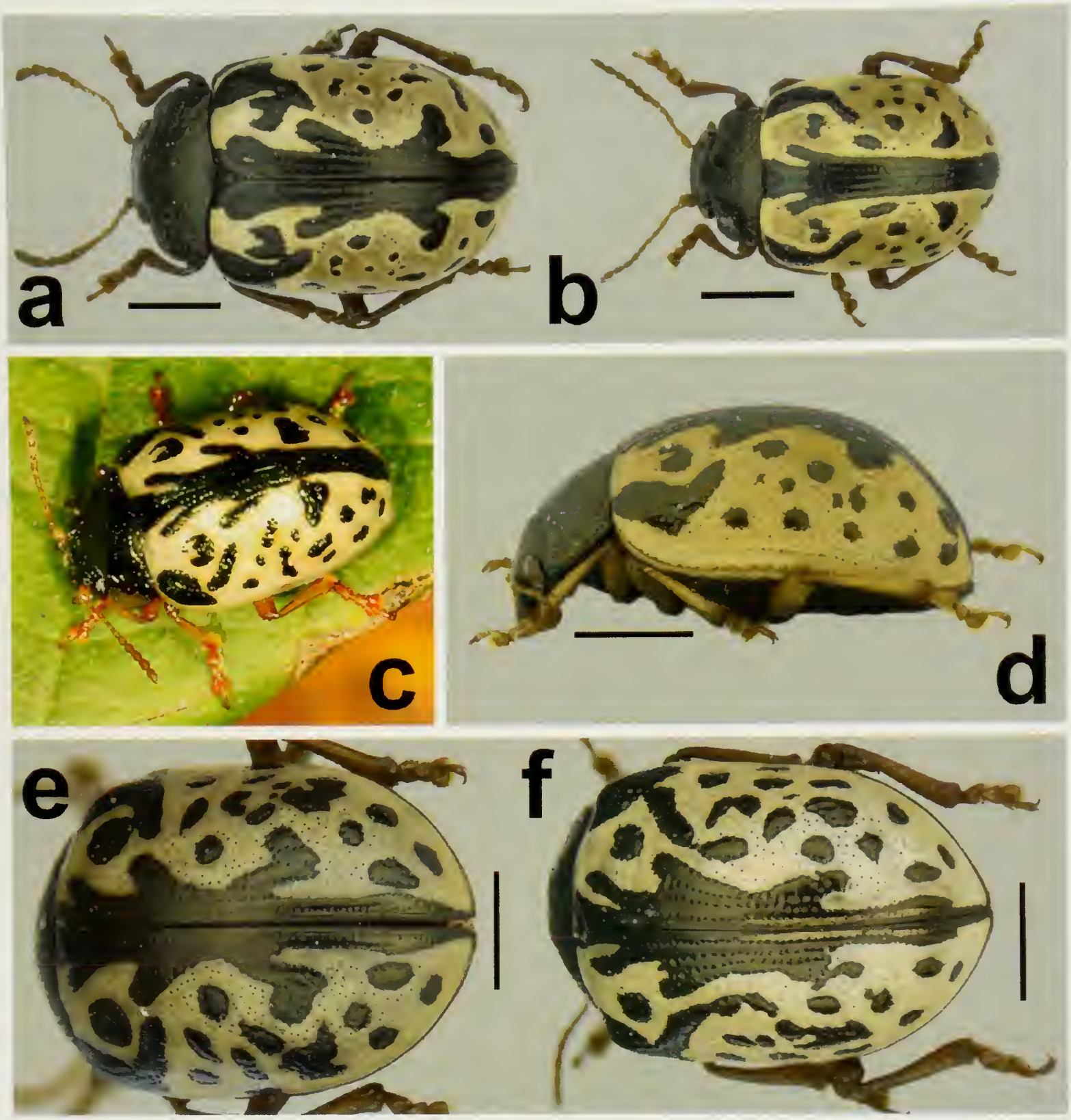

Figure 6. Habitus of different species in the "Calligrapha scalaris" group: a, *C. knabi* Brown (Canada: New Brunswick, Restigouche Co., Kedgwick, 2 June 2012, J. Gómez-Zurita, H. Vizán & T. Montelongo leg., IBE-JGZ voucher no. C479); b, *C. spiraea* (Say) (USA: West Virginia, Greenbrier Co., Tuckahoe Lake, 20 July 2001, J. Gómez-Zurita leg., IBE-JGZ voucher no. 114); c, living specimen of *C. dolosa* Brown with pale anterior angles of pronotum (picture by Tom Murray, under Creative Commons License and distributed by BugGuide, http://bugguide.net); d, lateral view of *C. rhoda* Knab (USA: New York, Saratoga Co., 7 August 2003, D. J. Funk leg., IBE-JGZ voucher no. 550); and apex of elytra of e, *C. virginea* Brown (USA: Wisconsin, Brown Co., Bayshore, 24 June 2010, J. Gómez-Zurita & T. Montelongo, IBE-JGZ voucher no. C134); and f, *C. confluens* Schaeffer (USA: New York, Essex Co., SW Wilmington, 25 May 2012, J. Gómez-Zurita, H. Vizán & T. Montelongo leg., IBE-JGZ voucher no. C505). Scale bars: 2.0 mm.

particular attention to the biology of the beetles, describing seven new species allied to *C. scalaris*. Interestingly, he had his own idea of *C. scalaris*, not based on the examination of LeConte's types, and his work based on northeastern North American beetles possibly rendered his elm-feeding *C. scalaris* not to be conspecific with LeConte's. This was a possibility contemplated by William Brown, who hoped that his species "represents, in part at least, LeConte's species" (Brown, 1945).

Having had the opportunity to work with LeConte's entomological collection at the Museum of Comparative Zoology (MCZ; Harvard University, Cambridge, Massachusetts), I tried to clarify in this work some of the taxonomic confusion surrounding the species *C. scalaris* by justifying the designation of a type specimen aiming at nomenclatural stability, redescribing the species on the basis of this type and providing some information on how to distinguish the species from allied taxa in what I present here as the "Calligrapha scalaris" group.

Neotype designation for *Calligrapha scalaris* (LeConte)

The conundrum about the identity of *C. scalaris* obviously requires the examination of LeConte's material, something that previous authors seem to have somehow neglected. The relevant type material is part of the beetle collection at the MCZ (Harvard Museum of Natural History, Cambridge, Massachusetts). It is currently represented by 28 pinned specimens distributed between LeConte's (10 specimens) and Horn's collections. The specimens used for the original description could be in any, as it is generally acknowledged that these entomologists shared their syntype series (P. D. Perkins, MCZ, personal communication). None of the specimens in LeConte's collection has locality data; only one specimen has a small blue circle pinned underneath the beetle, whereas in the other the circle is pink. The counterpart in Horn's collection includes eight specimens labeled "Can.", three as "Tex.", two as "N.H.", two as "Neb.", one as "N.C.", one as "Fla.", and one has no locality information. The explicit mention of several localities in the original description, from New York to Florida, is indicative of the existence of a syntype series, hopefully included among the specimens at hand, from which the type specimen should be designated to fix the species identity.

The first problem one faces, however, is that these 28 specimens represent as many as 9 or 10 different species that have been recognized by subsequent authors on the basis of sound morphological differences, as well as by different host plant associations, and all of them belong to the *C. scalaris* complex as identified by Brown (1945). This situation is revealed to be rather complex by the fact that LeConte's ill-defined species could indeed result in any or several of the younger names as synonyms. Not knowing what specimens this author used, it is possible to make a decision on how to typify his species preserving the maximum of information that has been accumulating in the literature (except perhaps for *C. scalaris* itself), as well as the taxonomic contributions by subsequent authors, preserving the stability of nomenclature. This can be accomplished by designating as type one of the specimens lacking morphological diagnostic characters for other easily recognizable taxa (not mentioned by LeConte, in any case), and that does not contradict the currently accepted idea of the association of *C. scalaris* with elm, regardless of LeConte's specimens being originally associated with this plant or not, since this information was not available to the author anyway. Proceeding with these goals in mind, the decision about type designation can be very much simplified and the effects on nomenclature reduced.

The series of 10 specimens from LeConte's collection shows dark epipleura; two of them (identified with little pink and blue circles) have them brown (Figs. 3a–c), and the other eight black with metallic sheen (Figs. 3d–f). These, together with other less conspicuous characters, clearly distinguish *C. ostryae* Brown, 1945 and *C. ignota*, respectively, from any other *Calligrapha* in this group. These two species were identified by Brown (1945) as specialists on hop-hornbeam (*Ostrya*) and birch (*Betula*), respectively. Five individuals from Canada in Horn's collection also show the black epipleura typical of *C. ignota*, a difference that was noted by this author, adding a label reading "epipl. virid." to one of the individuals. Horn's specimens also include two species that live associated with dogwood (*Cornus*), namely *Calligrapha floridana* (one exemplar, from Florida; Figs. 3g–i) and *C. rowena* (two individuals, from Canada; Figs. 3j–l). The former, as mentioned above, is perhaps the most similar externally among North American species to the elm-feeding *Calligrapha*, but its distribution in an important area of endemism in North America (Gómez-Zurita, 2005) and its host choice seemingly on *Cornus* allows us to treat it as a differentiated species, at least until new data become available. *Calligrapha rowena* is remarkably different from any other *C. scalaris*-like species (except *C. knabi*) in the shape of sutural and subsutural stripes, completely fused basally, with broad blunt lateral expansions below the scutellar area; heavy and basally emarginated spot enclosed by humeral lunule, sometimes confluent with inner margin of humeral lunule; arcuate band split in two short subtriangular oblique spots, the basal one completely fused to subsutural stripe and the apical one nearly always free; and very reduced additional markings on disc of elytra, which are relatively translucent at the apical two thirds to show the red color of wings when the insect is alive. Three of Horn's specimens, one from Canada and two from New Hampshire, can be ascribed without doubts to *C. confluens* (Figs. 4a–c), an alder (*Alnus*) specialist that can be recognized by its dark green metallic tint to head, pronotum, and elytral markings, the latter numerous, occupying most of the elytral surface compared with other species, showing irregular confluence patterns; subsutural stripe separated from sutural stripe for a relatively long distance basally, and the latter usually with a narrow depigmented area along suture on apical declivity of elytra; spot enclosed by humeral lunule large, ovoid, occupying a large space between lunule, subsutural stripe, and base of arcuate band; arcute band at wide obtuse angle with subsutural stripe, with apical half short, generally of irregular profile, perhaps confluent with surrounding markings; and midlateral spot free from elytral margin. The specimen from Nebraska (Figs. 4d–f) no doubt belongs to *C. rhoda*, distinguished by a roundish body, dark olivaceous tint to dark areas, and very characteristically by the double or transverse spot enclosed by humeral lunule; the shape of its arcuate band, as two narrow straight arms at wide-open obtuse angle, relate it to the form described as *C. rhoda walshiana* Knab, 1909. *C. rhoda* feeds exclusively on hazel (*Corylus*) throughout its range. One beetle, the smallest in the series and without locality data, strongly reminds one of the plum tree (*Prunus*) specialist, *Calligrapha pruni* Brown, 1945, as compared with this species' paratypes at MCZ (Figs. 4g–i). This species has a rotund body, slender humeral marking, small round spot enclosed by humeral lunule; rather straight, oblique arms of the arcuate band; relatively large midlateral spot, in most individuals narrowly separated from elytral margin; and in the case of the specimen at hand, rather reduced markings

on elytra. Finally, another specimen in this series and labeled "N. C." is a typical *Calligrapha dolosa* Brown, 1945 (Figs. 4j–l), as compared with Brown's types, and it has been associated with hawthorn (*Crataegus*). This specimen does not fit the original description by LeConte, in not having the "suture with a broad greenish blue denticulate line", since in this species, and particularly in the specimen at hand, the arcuate band, whose ends produce the "teeth" of the sutural stripe, is clearly detached from this stripe.

For the reasons exposed above, each one of the specimens mentioned can be discarded as potential lectotype for *Calligrapha scalaris*. The decision is thus restricted to four specimens, one from Nebraska and three from Texas, that still show some differences as to be considered two species. Among them, the ones from Texas have the greenish blue tinge to dark parts mentioned in the original description, not so apparent in the other specimen, which is slightly violaceous. However, the geographic provenance of these specimens generates an additional problem. Texas (or Nebraska) was not mentioned in the original description of *C. scalaris*. It is not possible to know whether John LeConte had these (or other) specimens from Texas at the time he proposed *C. scalaris*. However, in 1824, the year that the species was formally described, and until 1845 these territories were part of Mexico and still an exciting frontier of discovery for American naturalists. Therefore, it is highly unlikely that these specimens were in the entomologist's hands and that he did not highlight their provenance in his report, which basically described beetle species collected in Georgia (18 of 20). In these circumstances, there seems to be no suitable specimen to be designated as lectotype and at the same time preserving the stability of all subsequent taxonomic additions to North American *Calligrapha* since 1824. Yet, also relevant to making a decision, even though there is no host information for LeConte's and Horn's specimens, among the *C. scalaris*-like beetles known to live in Texas, at least one of them is reportedly feeding on elm. There is at least another locally abundant form that feeds on *Cornus* (personal observation; E. G. Riley, TAMUIC, personal communication), and it is indistinguishable from a morphological point of view from the *Ulmus* specialist. This could be a cryptic species, a host race, or the same species with an exceptionally broad trophic range, but at present we cannot ascertain its taxonomic status. In any case, by selecting one of the Texan specimens in the LeConte and Horn collections as the Neotype—very much consistent with the original description but also with the posterior usage of the name—unless it is possible to demonstrate that the specimens in the MCZ series actually belong to a *Cornus*-feeding species, *Calligrapha scalaris* (LeConte) will remain the elm Calligrapha beetle appearing in scientific literature but also in numerous forestry and agriculture reports (e.g., Dean, 1946). Besides, the small, roundish appearance of these beetles, as well as their reduced elytral markings, particularly the spot enclosed by humeral lunule, which in two of the individuals is a small round spot (Figs. 5a,b), approach the specimen figured by LeConte in his original work (Fig. 1a). The drawing inexplicably lacks the spot enclosed by lunule, otherwise a very prominent feature in every other *C. scalaris*-type forms (with the exception of *C. pruni*, see Figs. 4g–h and compare with Figs. 3g–h, for instance); thus it is difficult to understand that the author missed it if the example used was any of the other species. The specimens thus isolated to represent LeConte's species are, again with the exception of *C. pruni*, the smallest among potential syntypes. LeConte provided

data on size, giving half an inch as the size for this species; however, this information is not at all reliable, since the largest *Calligrapha* known to me is the Mexican *C. stillatipennis* Stål, 1859, nearly twice as big as many North American species, and it does not reach 12 mm.

A sound alternative that would take into account distribution information (Montelongo & Gómez-Zurita, in prep.) and morphological features would be selecting the specimen from Florida in the MCZ series as lectotype. But this decision would be destabilizing. Schaeffer's *C. floridana* would automatically become a junior synonym of *C. scalaris*, which would in turn become associated to *Cornus*, opposing more than 150 years since the ecological association with *Ulmus* was proposed. The elm Calligrapha would need formal description and a new name proposed. Instead, it seems advisable to retain the name associated to one of the specimens in LeConte's collection and consistent with its posterior usage.

Neotype designation for Calligrapha scalaris (LeConte). One female, Tex., Horn Coll. H6808, *Calligrapha scalaris* (LeConte) Neotype des. J. Gómez-Zurita 2010 (Fig. 5).

Paraneotypes. Two females, Tex., Horn Coll. H6808, *Calligrapha scalaris* (LeConte) Paraneotype J. Gómez-Zurita 2010.

Redescription of *Calligrapha scalaris* (LeConte)

The Neotype lacks six left apical antennomeres, the terminal segment of right antenna, right maxillary palp, left protarsus, and last three segments of left mesotarsus. Body oval, convex, 7.54 mm long, 4.75 mm wide (Figs. 5a–c). Head, most of mandibles, pronotum, and scutellum black with bluish metallic tinge; apex of mandibles, elytral markings, and ventral surfaces dark brown with slight bluish metallic shine; labrum, antennae, palpi, legs, internal margin of epipleura, and apical margin of last abdominal ventrite pale orangish brown; pale areas of elytra creamy yellow.

Head large, transverse, deeply inserted into pronotum; surface very finely shagreened, covered by rather dense strong punctures, except medially on frons before vertex; punctures near eyes with short anteriorly recumbent whitish setae, longer in depressed area above unpunctured supra-antennal calli; frons with fine longitudinal impression joining broad V-shaped frontoclypeal suture; area above eyes impressed by furrow prolonged for short distance beyond upper eye margin; space behind and below eyes coarsely punctured and with relatively long whitish setae; genae very short. Clypeus transverse, shagreened, strongly punctured at anterior half, with short, anteriorly recumbent pale setae; anterior margin at sides with longer, medially converging yellowish setae. Eyes relatively small, finely faceted, dorsoventrally elongated, entire. Labrum transverse, sides curved inward to broadly rounded anterior angles; apex weakly emarginate; transverse row of setigerous punctures in front of middle, with long, medially convergent yellowish setae. Mandibles large, strong, projecting beyond apical margin of labrum by more than 1.0× its length; sides concave before strong preapical curvature; surface densely covered by large setigerous punctures with long recumbent yellowish setae. Maxillary palpi slender; second palpomere long, with subcylindrical pedicel at basal half, gradually widening afterward toward apex; third palpomere long, base cylindrical, narrower than apex of previous segment, slightly elbowed and strongly widened toward apex; last segment subtrapezoidal, narrower at base and broadest preapically, before obliquely cut apex. Antennae slender, subclavate beyond fifth antennomere; scape

elongate oval, thick; pedicel subclavate, twice as long as wide at apex; third antennomere slender, twice as long as second; antennomeres 4–6 subequal, as long as but narrower than pedicel; antennomeres 7–10 short, nearly as long as wide at apex, strongly widened at base and weakly and gradually to apex afterward, densely setose.

Pronotum (Fig. 5d) very short, transverse, 0.45× shorter medially than wide between posterior angles; basal border at wide obtuse angle, broadly round medially, immargined; posterior angles obtuse; sides straight, subparallel, or very weakly convergent at basal 2/3, curving toward strongly produced anterior angle at apical 1/3; anterior border concave at angles, nearly straight medially; sides and apical border finely margined, with lateral margin not visible from above right behind anterior angles owing to strong pronotal convexity at anterolateral declivity; surface very finely microreticulated; punctuation double on disc, with denser, more or less homogeneously distributed minute punctures and sparse larger punctures, comparable with head punctures; sides of disc marked slightly ahead of middle by large, deep roundish hollows; punctures at sides stronger, deeper, larger than punctures on disc; lateral premarginal area with parallel row of deep punctures; deep longitudinally elongated punctures arranged near basal border. Hypomera rather flat, uniformly shagreened, unpunctured, with basal transverse impressions; hypomeral suture obliterated. Prosternum short, strongly transverse; anterior border concave, margined; disc and anterior half at sides microgranulated, unpunctured; posterior half before procoxae depressed, with strong, confluent punctures, setose; prosternal process convex medially, depressed at apex, punctured, with long pale yellowish setae mostly at sides and apex; process narrow between coxae, as wide as antennal scape, gradually widening toward straight cut apex; procoxal cavities open posteriorly. Mesanepisterna and mesepimera very finely microgranulose, unpunctured. Metanepisterna shagreened, densely covered by longitudinally elongated punctures, confluent alongside external margin. Mesoventrite transverse; space between mesocoxae convex, with fine yellowish setae. Metaventrite finely leathery, glossy on disc, finely impressed longitudinally, with sparse fine punctures and fine transverse scratches; sides finely shagreened, more densely punctured, punctures stronger near anterior angles; surface covered by sparse, very fine, short pale yellowish setae. Scutellum 1.14× longer than broad at base, lancet-shaped, sides tapering to blunt pointed apex; surface very finely microgranulose, unpunctured.

Elytra convex; base as broad as base of pronotum, humeri feebly protruding; sides weakly curved, maximum width at middle, apex commonly round; surface very finely microreticulated, smooth at external interval, densely and homogeneously covered by dot-like punctures, dark on paler areas; marginal interval unpunctured, limited internally by row of dot-like dark punctures parallel to elytral margin; punctures larger, deeper around and within dark areas. Markings as follows (Figs. 5a, b): (i) sutural stripe narrowly surrounding apical half of scutellum, narrow, entire, reaching sutural angle; (ii) basal end of subsutural stripe slightly behind apex of scutellum, weakly divergent and free from sutural stripe for length of four punctures, then completely confluent with it, nearly reaching sutural angle; slightly widened at apical declivity of elytra before gradually narrowing to apex; (iii) arcuate band consisting of two large spots fused laterally to dark interval confluent with subsutural stripe at middle 1/3 of elytra; basal spot shaped as elongated inverted tear, obliquely directed to suture, apical 2/3 confluent with subsutural stripe; apical spot

transverse, bean-shaped, convex apically, laterally confluent with subsutural stripe; (iv) humeral marking consisting of slightly curved elongated humeral spot, narrowly separated basally from base of elytra, nearly entirely confluent laterally with humeral lunule; lunule elongated, regularly concave internally, basally at level with humerus, and apical free end directed to suture and ending distant but level with basal end of arcuate band; (v) spot enclosed by humeral lunule small, roundish, placed behind midsection of humeral lunule, 0.5× closer to lunule than to subsutural stripe; (vi) midlateral spot larger than spot enclosed by lunule, longitudinally elongated, placed over premarginal line of punctures, occupying five punctures; laterally expanded toward elytral margin, without reaching it; (vii) spot of apical declivity as big as midlateral spot, roundish, completely fused laterally to preapical enlargement of subsutural stripe; (viii) apical spot round, small, equidistant from spot of apical declivity and margin of elytron (it appears as double spot on right elytron of neotype); (ix) 10 additional small round spots on disc of elytra, one on external concavity of arcuate band, four on lateral declivity evenly spaced between humeral and apical spots, more or less parallel to margin, and five on disc more or less evenly spaced in slightly wavy line between humeral lunule and spot of apical declivity. Epipleura smooth, unpunctured. Fully developed, reddish wings.

Femora straight, spindle-shaped, slightly enlarged medially; surface very finely shagreened, with sparse small punctures and short, adpressed yellowish translucent, very fine setae. Tibiae straight, gradually widening toward apex, as long and similarly sculptured as femora; apical half with semierect setae longitudinally on edges, dense at apex internally. Tarsi slender, shorter than tibiae; first tarsomere shorter than next two together; claws weakly divergent. Abdominal ventrites leathery on disc, very finely microgranulose at sides, rather densely punctured by small punctures with short, posteriorly recumbent very fine translucent setae; apical segment broadly round, with narrow premarginal furrow fringed with erect fine yellowish setae.

What is Brown's (1945) *Calligrapha scalaris?*

Fixing the meaning of *C. scalaris* (LeConte) to the small, round elm-feeding *Calligrapha* living in central and southern U.S.A. legitimates again the question implicit in Brown's (1945) work. Are the larger, more slender, more strongly pigmented elm-feeding *Calligrapha* in northeastern North America conspecific with the *C. scalaris* as recognized in the present study? Answering this question involves a thorough analysis of morphological variation in the species living on *Ulmus*, and a genetic study would certainly shed the required light to recognize whether these two (or more) forms can be considered as the same species, as sister species, or as independent adaptations to *Ulmus* as food source. Nonetheless, the degree of morphological variation observed between specimens reared on elm and named *C. scalaris* by Brown and the *C. scalaris* based on Horn's animals is as high as observed between different species (as assessed on the basis of their food choice as well as morphological differences; Brown, 1945). These differences may be compatible with treating both forms as different taxa, showing more or less consistent differences in their elytral markings, e.g., the size and position of the spot enclosed by humeral lunule.

The fact that under *C. scalaris* or more specifically, elm-feeding *Calligrapha*, there are several species that would provide an explanation for an observation by Robertson (1966) that was difficult to match with our current knowledge on the biology of these

beetles. Phylogenetic (Gómez-Zurita *et al.*, 2006) as well as genetic (Montelongo and Gómez-Zurita, 2015) studies on these beetles reinforce the idea that thelotoky arose several times independently in their evolution as a by-product of interspecific hybridization. As it occurs with many other animals, thelytoky appears in *Calligrapha* associated with polyploidy (Robertson, 1966). Yet, a few species in *Calligrapha*, including *C. scalaris*, were reported as facultatively parthenogenetic for showing some female-only populations or at least those with highly distorted sex ratios (Brown, 1945; Robertson, 1966). Indeed, all other unisexual species in the genus are reproductively isolated from their bisexual counterparts not only by a different reproductive strategy, but also owing to insurmountable genomic imbalances due to the hypothesized polyploid hybrid genomic structure in these species (Montelongo & Gómez-Zurita, 2015). Thus, it becomes somewhat of a problem to accept that this really complex mechanism can be polymorphic in one species, e.g., *C. scalaris*. A more parsimonious and plausible explanation of these observations is that there are at least two species of *Calligrapha* associated with *Ulmus*, probably more, and some of them, including some Canadian and Kansas populations studied by Brown (1945) and Robertson (1966), thelytokous.

Regardless of differences in their reproductive biology, which, if confirmed, would strongly support the case of different elm-feeding species, the decision on the taxonomic status of Brown's concept of *C. scalaris* can be adjourned until new data become available.

Diagnosis of *Calligrapha scalaris* (LeConte)

The drawings for *C. scalaris* (LeConte) provided by previous authors do not conform to the concept for this species put forward here, on the basis of the study of LeConte's specimens. For instance, Rogers (1857) shows a beetle that could represent any of the *C. scalaris*-type beetles, but not the southern elm-adapted forms, particularly in that the beetle portrayed is more slender and it has the spot enclosed by humeral lunule large. The same is true for the specimen figured in Jacoby's (1880–1892) monograph. Other drawings, particularly the one by E. Knobel (1895) used by him and subsequent authors to describe the species (e.g., Blatchley, 1910; Downie and Arnett, 1996), lack sufficient detail to make a reliable identification.

When ecological information is not available, there are at least two species that can be readily identified thanks to conspicuous diagnostic character states about the color of their elytral epipleura. These are *C. ignota*, a birch-feeding species that shows blackish epipleura with metallic sheen (Fig. 3f), and *C. ostryae*, a hop-hornbeam-feeding species with brownish epipleura (Fig. 3c). The next character that is worth looking at is the configuration of the midlateral spot (Fig. 2), either broadly confluent with elytral epipleura, or detached from elytral margin (or narrowly confluent, at most). The specimens identified as *C. scalaris* have this spot placed medially on elytra, over the midlateral line of punctures, expanded toward elytral margin, but reaching it narrowly, if at all (Fig. 5b). This trait can be important to distinguish the elm-feeding *Calligrapha* from the birch and hop-hornbeam species, but also from other species that lack the diagnostically dark epipleura, such as *C. floridana* (Fig. 3g), *C. knabi*, *C. tiliae* Brown, 1945, or *C. virginea* Brown, 1945, two dogwood and two linden specialists, respectively, otherwise very much "scalaris"-like. The midlateral spot is frequently missing in *C. rhoda* (Fig. 6d); thus it is also a good character to use to diagnose this species and differentiate it from *C. scalaris* and any other species in this group. However, those *C. rhoda* specimens with

midlateral spot can still be easily differentiated from *C. scalaris* by their double spot enclosed by humeral lunule (sometimes both spots are confluent in a U-shaped or transversal spot), their dark olive-brownish tinge to dark parts, as opposed to bluish green in *C. scalaris*, and their stronger body puncturation, giving a somehow rough appearance to dorsal surfaces (Figs. 4d, e). Another distinctive feature of *C. scalaris* is the well-developed arcuate band, producing the characteristic dentate shape of the sutural marking described by LeConte (1824). The presence of this band, with marked basal and apical lobes, the latter rather big, transverse, sometimes V-shaped (Fig. 5a), is shared by several species in the group, but readily distinguishes *C. scalaris* from *C. dolosa* and *C. rowena* (apical lobe detached from sutural stripe; Figs. 3k and 4k), *C. rhoda walshiana* (apical lobe narrow linear, slightly divergent from suture, sometimes free; Fig. 4e), *C. confluens* (apical lobe straight, short, of irregular profile; Fig. 4b), and *C. spiraea* (Say, 1826) (lacks the apical lobe; Fig. 6b). The spot of apical declivity (Fig. 2) on elytra tends to be broadly confluent with subsutural stripe in *C. scalaris*, which should help differentiate it again from *C. confluens*, *C. ignota, C. knabi, C. pruni, C. rhoda walshiana, C. rowena*, and *C. virginea*, where this spot tends to be free. The humeral marking (Fig. 2) in *C. scalaris* seems smaller, more compact than in other species in the group, with the apex of humeral lunule reaching at level or only slightly beyond the extreme basal end of the arcuate band (Figs. 5a, b). In other species this marking is more slender, reaching for a short distance beyond the basal end of the arcuate band, as can be seen in *C. confluens, C. ignota*, *C. pruni, C. tiliae*, or *C. virginea*, and it is heavier, as in *C. amator* Brown, 1945 and most others, except perhaps *C. pruni*. The same is true for the spot enclosed by humeral lunule, relatively small in *C. scalaris, C. pruni*, and *C. rhoda*, but large, occupying a big proportion of the space delimited by humeral lunule, basal end of arcuate band, and divergent base of subsutural stripe in the other species, with a distance from the spot to any of these features never larger than the diameter of the spot.

With this information, it is possible to produce a tentative key to identify the species in the "Calligrapha scalaris group" on the basis of practical differences that apply to a large proportion of individuals (at least those generally matching the phenotype of the respective types), even though not trying to reflect the relationship of the species involved. In general terms, it would be possible to recognize the "C. scalaris group" as these species showing elytra with the subsutural stripe confluent with sutural stripe and also with one (typically the basal one) or both spots in which the arcuate band is divided (except in *C. spiraea*, where this last feature is free; Fig. 6b). The other group or groups of related North American *Calligrapha*, tentatively proposed here under the name "Calligrapha philadelphica" group, have these three features nearly always free (in *C. vicina* Schaeffer, 1933 and *C. suturella* Schaeffer, 1933 sutural and subsutural stripes are confluent). The key is based in the examination of type specimens; thus it is expected to help identify most individuals. However, since the proposed key is generally based on the elytral markings and we know that *Calligrapha* has a tendency to variation in these markings, it is possible that a certain proportion will fail to be keyed out or will actually result in a wrong identification.

Identification Key of *Calligrapha* Chevrolat Species in the "Calligrapha scalaris" Group:

1a. Midlateral spot absent (Fig. 6d); found on hazel (*Corylus*) . . . . . *Calligrapha rhoda* Knab (pars)

1b. Midlateral spot present (Figs. 3a, d, g, j, 4a, d, g, j, and 5b) 2
2a. Dark epipleura (Figs. 3c, f) 3
2b. Pale epipleura (Figs. 3i, l, 4c, f, i, l, and 5c) . . . 4
3a. Black epipleura (Fig. 3f); found on birch (*Betula*) . . . . . *C. ignota* Brown (Figs. 3d–f)
3b. Brown epipleura (Fig. 3c); found on hop-hornbeam (*Ostrya*) . . . . . *C. ostryae* Brown (Figs. 3a–c)
4a. Pale anterior angles of pronotum (Fig. 6c); found on hawthorn (*Crataegus*) . . . . . *Calligrapha dolosa* Brown (pars)
4b. Dark anterior angles of pronotum (Fig. 5d) 5
5a. Midlateral spot broadly confluent with margin of elytron (Fig. 3g) 6
5b. Midlateral spot narrowly confluent or free from elytral margin (Figs. 4a, d, g, j, and 5b) 8
6a. Spot of apical declivity free from subsutural stripe (Fig. 6e); found on linden (*Tilia*) . . . . . *C. virginea* Brown
6b. Spot of apical declivity confluent with subsutural stripe 7
7a. Humeral marking free from base of elytron (Fig. 5d); found on linden (*Tilia*) . . . . . *C. tiliae* Brown
7b. Humeral marking broadly connected anteriorly to base of elytron (Fig. 3g); found on *Cornus* . . . . . *Calligrapha floridana* Schaeffer
8a. Spot enclosed by humeral lunule double, with both spots free, fused as a transverse or U-shaped marking, but always relatively small (Figs. 4e, 5a, 6b, d) 9
8b. Spot enclosed by humeral lunule single, round, oval, transverse, maybe slightly emarginated anteriorly (Fig. 4h), or if double or U-shaped, then relatively big (Figs. 3k, 6a) 10
9a. Arcuate band confluent with subsutural stripe; found on hazel (*Corylus*) . . . . . *Calligrapha rhoda* Knab (pars) (Figs. 4d–f)
9b. Arcuate band reduced to two spots free from subsutural stripe; found on ninebark (*Physocarpus*) . . . . . *C. spiraea* (Say) (Fig. 6b)
10a. Spot enclosed by humeral lunule removed from subsutural stripe by distance over 1.0× width of spot (Figs. 4h, 5a) 11
10b. Spot enclosed by humeral lunule at most as far as 1.0× its width from subsutural stripe, usually much less (Figs. 3h, k, 4b, k, 6a, c, e, f) 12
11a. Spot of apical declivity of elytra free or narrowly connected to subsutural stripe; brownish or bronzy greenish tinge to head, pronotum, and dark markings; found on wild plum (*Prunus*) . . . . . *C. pruni* Brown (Figs. 4g–i)
11b. Spot of apical declivity of elytra generally confluent with subsutural stripe; bluish green tinge to dark body parts; found on elm (*Ulmus*) . . . . . *C. scalaris* (LeConte) (Fig. 5)
12a. Apical arm of arcuate band generally detached from subsutural stripe (Figs. 3k, 4k) 13
12b. Apical arm of arcuate band always confluent with subsutural stripe (Figs. 4b, 5a, 6a, e) 14
13a. Base of subsutural stripe divergent from sutural stripe; large additional spots on disc of elytra; found on hawthorn (*Crataegus*) . . . . . *Calligrapha dolosa* Brown (pars) (Figs. 4j–l)
13b. Base of subsutural stripe entirely confluent with sutural stripe; small additional spots on disc of elytra; found on dogwood (*Cornus*) . . . . . *Calligrapha rowena* Knab (Figs. 3j–l)
14a. Base of subsutural stripe completely confluent with sutural stripe; found on dogwood (*Cornus*) . . . . . *Calligrapha knabi* Brown (Fig. 6a).
14b. Base of subsutural stripe divergent from sututral stripe if for a short distance (Figs. 4b, 5a) 15
15a. Suture narrowly pale at apical declivity of elytra (Fig. 6f); found on alder (*Alnus*) . . . . . *C. confluens* Schaeffer (pars)
15b. Suture completely dark along its whole length . . . 16
16a. Apex of arcuate band short, weakly divergent from subsutural stripe, of irregular profile (Fig. 6f), usually confluent with surrounding spots; dark green metallic tinge to dark areas; found on alder (*Alnus*) . . . . . *C. confluens* Schaeffer (pars) (Figs. 4a–c)
16b. Apex of arcuate band longer, divergent from subsutural stripe, V-shaped or more or less neatly round; bluish black metallic tinge to dark areas; found on linden (*Tilia*) . . . . . *C. amator* Brown

On the meaning of *Calligrapha multiguttis* Stål, 1865

After several years studying American Chrysomelinae, the Swedish entomologist Carl Stål (1865) failed to discover fixed diagnostic differences that unambiguously separated several of the genera dealt with in his monograph, including *Calligrapha*. Thus he lumped them under the Linnean genus *Chrysomela*, resulting in some homonymies that he disambiguated. Unfortunately, one of them affected precisely LeConte's taxon *C. scalaris*. Stål's (1865) naming exercise, with the proposition of *C. multiguttis* to represent LeConte's species, was accompanied by a redescription based on a series of

specimens presumably in the beetle collections of Berlin and Stockholm. It is possible to recognize the use of several specimens for this redescription based on the mention of at least two depositories, and it becomes clear that more than one specimen was used according, for instance, to the description of the spot of apical declivity close to subsutural stripe or sometimes (interdum) confluent with it. Knowing the circumstances around the name *C. scalaris* (LeConte), it seems important to try to understand Stål's concept of this species, and therefore the meaning of *C. multiguttis*. I could not localize the specimen(s) at the Naturhistoriska riksmuseet (Stockholm, Sweden), which hosts Stål's collection. They could have been arranged among other *C. scalaris* by Stål himself, curator of this part of the collection. However, the original series has been preserved and identified at the Museum für Naturkunde (Berlin, Germany), slightly complicating the picture of what represents the name *C. multiguttis* and how it relates to *C. scalaris*. Indeed, the examination of this series of six specimens (Nr. 29806 in the MfN Collection registry) reveals that it includes at least five species, all of them in what could be considered the "scalaris-complex", similarly as it happens with LeConte's and Horn's collections. The series opens with one specimen labeled as "29806, scalaris Rog. Suffr.*, Amer. Sept.", which fits the description and appearance of *C. floridana*, with midlateral spot broadly confluent with elytral margin, as well as spots of apical declivity fused with subsutural stripe. An unlabeled specimen with similar characteristics but with the humeral marking free from elytral margin basally could be referred to *C. tiliae*. Another unlabeled specimen has conspicuous black epipleura; thus it belongs in *C. ignota*. Yet another unlabeled specimen, smaller, with large midlateral spot and free spots on apical declivity of elytra, is typical for *C. knabi*. Fortunately for the stability of current nomenclature, one unlabeled specimen and the one closing the series, with the label "scalaris Rog. Suff.*, Texas, Friedr.", have very reduced markings, typical of *C. scalaris* as interpreted in this work, particularly by the spot enclosed by humeral lunule small and conspicuously closer to humeral lunule than to subsutural stripe, as well as free midlateral spot. However, these specimens show a free spot of apical declivity, approaching *C. pruni* instead, and in any case cautioning about the use of this character as diagnostic of these taxa. With this information at hand it is possible to split the synonymy for the different taxa involved: *C. scalaris* (LeConte) (= *Chrysomela multiguttis* Stål, 1865 [pars], Mon. Chrys. Am., iii, p. 261), *C. ignota* Brown (= *Chrysomela multiguttis* Stål, 1865 [pars] **nov. syn.**, Mon. Chrys. Am., iii, p. 261), *C. knabi* Brown (= *Chrysomela multiguttis* Stål, 1865 [pars] **nov. syn.**, Mon. Chrys. Am., iii, p. 261), and *C. tiliae* Brown (= *Chrysomela multiguttis* Stål, 1865 [pars] **nov. syn.**, Mon. Chrys. Am., iii, p. 261).

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